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One nest of *Sceliphron*
madraspatanum (Fabr.) (Sphecidae;
Hymenoptera)

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(With 18 figures in four plates)

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I. INTRODUCTION

This paper describes the building of a nest by one female of the species *Sceliphron madraspatanum* (Fabr.), during 14 days, on 12 of which it is unlikely that a visit was unnoted. Visits to the construct and absences were described and timed to the nearest second. Such a crudely biometrical approach, which we do not think has been attempted before, we hope compensates for the qualitative gaps in the record due to the observers' ignorance of the Hymenoptera at the time the opportunity to collect these data presented itself.

The record was made by H.S. and K.R.D.; S.D.J. made the statistical analysis and the excavation and interpretation both of this nest

and corpses, and of that found in 1961. Professor J. B. S. Haldane assisted with both the collection and the analysis of the data. Dr. J. van der Vecht of Leiden identified our specimens, and with Dr. E. White of Liverpool and Dr. Kenneth W. Cooper of Dartmouth, New Hampshire, introduced us to the literature. We wish to thank all these collaborators.

II. THE SEQUENCE

The nest was built between 15-7-1960 and 28-7-1960 in a house just north of the Calcutta municipal boundary. It is in a rapidly developing industrial area but still surrounded on all sides by waste grassland intersected by ditches. In July, which is during the first half of the monsoon, all soil is almost continuously muddy. A small varnished wooden table 60 cm. high and 75×33 sq. cm. in area stood against the west wall of a first floor (in the English sense, not ground floor) room about one metre from a permanently open window in the north wall. The nest was built about 7 cm. from the north-east corner of the table immediately under the horizontal table top on the vertical bar of wood supporting this, on the side of the table facing east. A chair stood in the NW. corner of the room between the table and the window. During the period of observation the time of sunrise advanced from 05.01 to 05.06 and sunset retreated from 18.24 to 18.19 Indian Standard Time. Noon, therefore, was about 11.42. The temperatures were not recorded in the room of observation; but in a similar shaded room, but permanently open to the south, the maximum and minimum temperatures recorded between 12.00 and 13.00 on 15/7 for the last 24 hours were 28.8° and 26.3°C . They were not recorded on 16/7 and for the rest of the period of observation were always between 30° and 31° and 27.7° and 28.9° respectively.

15/7. Sometime after 09.00 a reader in the above-mentioned chair was disturbed by an insect repeatedly flying across the page of the book. Note taking was begun at 09.24. After two visits it was realized that intervals must be recorded to the nearest second. When, after about 4 minutes, the table was inspected during an absence, a smooth layer of mud, in the centre of which was a small cup, was seen. Records were kept of the rest of the construction of the walls of cell I, which was finished at 10.06.59, i.e. 59 seconds after 10.06 a.m. (Fig. 1.). No further visit was recorded until 11.44, when watching was discontinued. At 11.46 or 47 the nest was again inspected, and at 11.48.45 the wasp returned and entered the tube completely.

Oviposition is thought to take place during this complete entry. No load was seen on 15/7, though comparison with subsequent

cells makes it virtually certain that the wasp entered carrying a spider. Watching was recommenced, the observer sitting opposite the nest. The observer sat in this position for all subsequent observation of the nest. Six further visits were observed, and no loads were seen. It seems possible, on interpreting the actual wording of the notes afterwards, that loads were brought on three of these. That no spiders were seen is interpreted as due to the observer (H.S.) expecting the wasp to bring Lepidopteran caterpillars and therefore being insufficiently attentive to observe less conspicuous objects. Two visits were occupied with closing the cell with mud making a *concave* lid. At 14.47, an hour after the second lid building visit, watching was discontinued for the day. In the evening no further construction was noted, so only visits for inspection can have been missed. The afternoon was sunny.

16/7. At 07.47 the wasp was noticed flying round the nest. At 07.52 disciplined observation was begun. The concave lid was already removed from cell I. At 08.09.24 the animal settled for the first time. After 3 more visits, during which no load was seen, one spider was introduced. Then the cell was sealed with a *convex*, almost knob-like, smooth lid made with mud brought on 3 journeys, and 2 loads of mud were daubed on each side of it immediately. The wasp then smoothed mud on the table immediately below cell I. This smoothing stopped for a period of over half an hour. It recommenced, and upon the smoothed mud she built cell II (Fig. 2). During this period we first noticed that the cell walls were made by bringing balls of mud which were placed in the centre of the existing arch and rolled out towards the surface of the table with the mandibles and the 1st pair of tarsi. One of each pair of appendages worked against the inner and one against the outer surface of the cell, therefore they made little ridges in the soft mud of the temporary margin, at right angles to the line in which the balls were being extended. After the first rolling out, the newly applied mud was reworked by the same movements several times up to the vertex of the arch and down to the floor. The balls were rolled out first to the right and then to the left. Therefore strips were added to each wall more or less alternately. The alternation with which the two sides of the wall were built was almost complete for cells II and III which like cell I lay flat upon the vertical surface of the table. Later cells were built behind these first three, propped up against them so that they were at an angle with the vertical support of the table top. These later cells were fitted into the uneven foundation, and their walls were curved to fit awkward niches by rolling out several balls parallel to one another on the same side of the vault one after another. The cell wall was always begun on a *foundation* of mud smoothed on the table, and from the beginning of the cell itself, the walls were built

by rolling out loads in an alternating way. Each cell was thus an arched vault, the whole floor of which in the early cells, and of the base of the later cells, was mud smoothed upon the vertical wood, but the floor of most of the length of the later cells was a previously made part of the construct. When a cell was about 2.2 cm. long the mud balls were rolled in such a way that the floor space left between the walls gradually narrowed until the two walls met and a short cylindrical neck was formed, finished off with a rim. The cells are thus about 0.5 cm. less in length than those of the species described by Fabre which Berland (1925) identified as *S. spirifex*, and the spiders introduced are correspondingly smaller (Fabre 1924) but our animal similarly buzzed during building. After rolling each ball on to the cell, the wasp swept it vigorously with her antennae, both inside and out, but she never applied any pressure or moulded the mud with the antennae. She repeatedly cleaned her antennae and mouth-parts with her front tarsi. Some of these details are from notes taken during later periods of cell building. It will be noticed from Table III that the fewest wall building visits are recorded for cell II. This is perhaps because wall building was not at first distinguished from foundation building. While fetching mud the wasp did not always fly in the same direction when leaving the window, nor did she arrive from only one direction.

After 391 seconds the wasp returned with a spider, entered cell II, abdomen first, and entered it completely. She emerged head first and flew. The spider was dragged out hanging from her by its silk, fell to the ground and was retrieved by the observer. It did not move and was preserved. The wasp returned after 2316 seconds, again with a spider, and again she entered backwards and completely. On 22/7 again she pulled out the spider after this backwards entrance to cell VII, and again repeated the same procedure on her next visit. She entered both backwards and entirely only once into all the other cells. All other spiders were thrust in with the head and forelegs, the abdomen being clearly visible throughout the process. No spider inserted in this way was ever dragged out, though in filling cell VII one was too large and escaped, only to fall motionless to the ground immediately. The complete entrance was the only activity on the nest in which the abdomen was completely hidden from the observer for more than an instant. We assume the oviposition to take place during this complete entrance, both because of its quite discrete difference from other spider-bringing visits and because previous describers of this and other species of *Sceliphron* assume that the eggs, which are attached to a spider, are laid inside the cell and not at capture, or during transportation to the cell. If this interpretation is correct this individual of *S. madraspatanum* like those described by Horne

(1872) and Dutt (1913) was unlike *S. caementarium* (the Peckhams 1905 and Shafer 1949) but like *S. (Pelopaeus) spirifex* (Fabre 1924) in laying her egg invariably on the first spider. Oviposition seemed to miscarry surprisingly often, but the animal seemed able to compensate for these miscarriages by repeating the process. On 16/7 watching was discontinued from 11.47 to 14.00. When the observers returned, cell II was sealed with a concave lid, and cell I was covered with a shapeless mass of roughcast which was dark and therefore damp when first seen (Fig. 3). Watching was continued until 18.07, and though the afternoon was sunny, only one visit, which was without a load, was observed. Probably less than 40 visits were missed.

During the whole 14 days of observation 91 visits were observed, during which we are certain the animal neither brought provisions nor altered the construct. These 91 are called *inspections*. During them she swept the construct with her antennae, which she wiped with her first pair of tarsi at intervals. This *sweeping* was also performed during almost all other visits. The antennae were swept up and down the edges and the interior of the half-built cells, and, we think, wiped more often than usual with the feet during this activity. More than half of these inspections took place while the cell was being provisioned, when the antennae and sometimes the head and thorax were thrust into the open cell. The wasp rarely entered an open cell. This sweeping would seem to have been a scanning activity by which the wasp received stimuli, or information, from the nest. The wiping with the tarsi may have merely cleaned the antennae, but may also have been important sensorily, by bringing particles picked up by antennae into contact with sense organs on the legs.

17/7. From 17/7 we in turn attempted to watch throughout the possible working day of a wasp; and if any visits were missed, they must have been visits of inspection only. The 2nd and 3rd columns of Table I give the time of the observer's arrival and the wasp's first arrival respectively. Columns 16 and 17 give the corresponding times of the wasp's and the observer's last departure. On 17/7 the animal swept the construct for less than 2 minutes of the first visit, paying special attention to the concave lid of II but also to the undaubed table top. Then she bit small fragments of mud from around the edge of the concave lid. She continued this with 4 pauses, one of 3 minutes, until the lid fell off as a little disc. She then swept inside

TABLE
VISITS OF *Sceliphron madraspatanum*

Date	Watch begun	1st arrival	First inspections	Foundation	Wall	Oviposition	Prey	Doubtful prey		
1	2	3	4	5	6	7	8	9		
15/7	— 09.24	— —	? —	x on I —	x on I 25(+2) on I	— —	— —	— —		
	— 11.47	— 11.48.45	? —	— —	— —	— 1 in I	— —	— 3 in I+3		
16/7	— 07.30	— 08.09.24	? ?	— —	— —	— —	— ? in I	— 5 in I		
	— —	— —	— —	— 9 on II+3	— 22 on II	— 2 in II	— 1 in I	— —		
	— 14.00	— 14.44.50	— —	— —	— —	— —	— ? in II + ?	— —		
17/7	06.14	09.13.22	0	—	—	—	—	—		
	—	—	—	—	—	—	3 in II + 3	1 in II+2		
18/7	06 52	09.07.03	0	—	—	—	—	—		
	—	—	—	13 on III	24 on III	—	3 in II + 8	—		
19/7	07.15	08.48.50	2	—	—	1 in III	4 in III + 2	1 in III		
	—	—	—	5 on IV	27 on IV	—	—	—		
20/7	07.12	07.54.25	2	—	1 on IV	1 in IV	2 in IV + 2	2 in IV		
	—	—	—	1 on V	—	—	—	—		
21/7	06.43	07.07.06	1	—	—	—	—	—		
	—	—	—	19 on V+1	29 on V	1 in V	8 in V + 2	2 in V		
22/7	06.13	07.04.03	1	5 on VI	25 on VI	1 in VI	5 in VI + 2	—		
	—	—	—	11 on VII+1	26 on VII	2 in VII	1 in VII	—		
23/7	06.11	08.07.13	0	—	—	—	—	—		
	—	—	—	—	—	—	3 in VII+2	3 in VII		
24/7	06.30	07.41.35	1	—	—	—	—	—		
	—	—	—	1 on VIII	30 on VIII	1 in VIII	11 in VIII+3	1 in VIII		
	—	—	—	2 on IX+1	25 on IX	—	—	—		
25/7	06.23	07.29.25	1	—	—	1 in IX	1 in IX+4	—		
	—	—	—	4 on X	—	—	—	—		
26/7	06.23	07.08.17	1	—	—	—	—	—		
	—	—	—	10 on X+1	29 on X+2	—	7 in IX + 4	1 in IX+1		
27/7	06.10	07.31.30	1	—	—	1 in X	4 in X + 7	—		
28/7	06.39	?	?	—	—	—	—	—		
	—	—	—	—	—	—	2 in X + 5	—		
	—	—	10	80	7	263(+2) 2	12	51 spiders 44 + 3 flies + 1 spider escaped	19	6

NOTE. Numbers in brackets visits counted but not timed. Numbers in italics inspections are listed separately.

I
(FABR.) TO NEST UNDER CONSTRUCTION

Concave lid	Removal of lid	Convex lid	Daub	Smooth	Last inspections	Last Departure	End of Watch	Totals	
10	11	12	13	14	15	16	17	18	
—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	10.06.59	11.44	—	—
2 on I	—	—	—	—	—	13.46.30	14.47	—	—
—	—	—	—	—	?	—	—	31(+2)	3+ x
—	x from I	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—
—	—	5 on I	—	—	—	—	—	—	—
x on II+?	—	—	x	—	—	11.45.37	11.47	—	—
—	—	—	—	—	?	14.46.05	18.07	44	4+ x
2 on II+?	1 from II	—	—	—	—	—	—	—	—
—	—	—	—	—	0	14.29.20	18.15	7	6
—	1 from II	—	—	—	—	—	—	—	—
—	—	7 on II+2	29	1	—	—	—	—	—
—	—	—	—	—	0	16.51.38	18.21	78	10
—	—	6 on III	—	1	—	—	—	—	—
—	—	—	—	—	?	17.20.59	18.46	45	5
—	—	8(+1) on IV+2(+2)	12	2	—	—	—	—	—
—	—	—	—	—	0	14.47.11	18.23	29(+1)	6(+2)
—	—	1 on IV	32(+1)	13	—	—	—	—	—
—	—	12 on V	—	—	—	16.23.45	18.46	117(+1)	4
1 on VII	—	10 on VI	5	1	—	—	—	—	—
—	—	—	80+3	34	0	17.14.30	18.32	207	7
—	1 from VII	—	—	—	—	—	—	—	—
—	—	4 on VII+?	—	—	0	10.40.46	18.45	11	3
—	—	3 on VII	1	—	—	—	—	—	—
—	—	6 on VIII	1	—	—	—	—	—	—
—	—	—	—	—	0	15.53.28	18.32	82	5
2 on IX+?	—	—	—	—	—	—	—	—	—
—	—	—	57+4	4	2	17.29.31	18.43	69	12
—	1 from IX	—	—	—	—	—	—	—	—
—	—	9 on IX	6	—	—	—	—	—	—
—	—	—	—	—	?	17.01.08	18.32	63	10
2 on X+?	—	—	53+?	13	—	15.46.32	18.30	73	10
—	(+1)+1 from X	—	—	—	—	—	—	—	—
—	—	—	—	—	—	11.39.31	18.34	3(+1)	5
9	34(+1)+ x	71(+1) 5(+2)	276(+1) 8	69	5	—	—	—	90(+2)

immediately before and during relevant activity, except for first and last inspections of day which

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1	2	3	4	5	6	7	8	9		
15/7	09.24	—	<i>?</i>	x on I	x on I 25(+2) on I	—	—	—		
	11.47	11.48.45	<i>?</i>	—	—	1 in I	—	3 in I+3		
16/7	07.30	08.09.24	<i>?</i>	—	—	—	? in I	5 in I		
	14.00	14.44.50	—	9 on II+3	22 on II	2 in II	1 in I	—		
			—	—	—	—	? in II + ?	—		
17/7	06.14	09.13.22	0	—	—	—	3 in II + 3	1 in II + 2		
18/7	06.52	09.07.03	0	—	—	—	3 in II + 8	—		
			—	13 on III	24 on III	—	—	—		
19/7	07.15	08.48.50	2	5 on IV	27 on IV	1 in III	4 in III + 2	1 in III		
20/7	07.12	07.54.25	2	1 on V	—	1 in IV	2 in IV + 2	2 in IV		
21/7	06.43	07.07.06	<i>I</i>	19 on V+ <i>I</i>	29 on V	1 in V	8 in V + 2	2 in V		
22/7	06.13	07.04.03	<i>I</i>	5 on VI 11 on VII+ <i>I</i>	25 on VI 26 on VII	1 in VI 2 in VII	5 in VI + 2 1 in VII	—		
23/7	06.11	08.07.13	0	—	—	—	3 in VII+2	3 in VII		
24/7	06.30	07.41.35	<i>I</i>	1 on VIII 2 on IX+ <i>I</i>	30 on VIII 25 on IX	1 in VIII	11 in VIII+3	1 in VIII		
25/7	06.23	07.29.25	<i>I</i>	4 on X	—	1 in IX	1 in IX+4	—		
26/7	06.23	07.08.17	<i>I</i>	10 on X+ <i>I</i>	29 on X+2	—	7 in IX+4	1 in IX+ <i>I</i>		
27/7	06.10	07.31.30	<i>I</i>	—	—	1 in X	4 in X + 7	—		
28/7	06.39	<i>?</i>	<i>?</i>	—	—	—	2 in X + 5	—		
	—	—	<i>10</i>	80	7	263(+2) <i>2</i>	12	51 spiders 44 + 3 flies + 1 spider escaped	19	6

NOTE. Numbers in brackets visits counted but not timed. Numbers in italics inspections are listed separately.

I

(FABR.) TO NEST UNDER CONSTRUCTION

Concave lid	Removal of lid	Convex lid	Daub	Smooth	Last inspections	Last Departure	End of Watch	Totals
10	11	12	13	14	15	16	17	18
—	—	—	—	—	—	10.06.59	11.44	—
2 on I	—	—	—	—	—	13.46.30	14.47	31(+2)
—	x from I	—	—	—	<i>?</i>	—	—	3+ x
—	—	5 on I	—	—	—	11.45.37	11.47	—
x on II+ <i>?</i>	—	—	x	—	<i>I</i>	14.46.05	18.07	44
2 on II+ <i>I</i>	1 from II	—	—	—	0	14.29.20	18.15	7
—	1 from II	7 on II+2	29	1	0	16.51.38	18.21	78
—	—	6 on III	—	1	<i>I</i>	17.20.59	18.46	45
—	—	8(+1) on IV+2(+2)	12	2	0	14.47.11	18.23	29(+1)
—	—	1 on IV 12 on V	32(+1)	13	—	16.23.45	18.46	117(+1)
1 on VII	—	10 on VI	5 80+3	1 34	0	17.14.30	18.32	207
—	1 from VII	4 on VII+ <i>I</i>	—	—	0	10.40.46	18.45	11
—	—	3 on VII 6 on VIII	1 1	—	0	15.53.28	18.32	82
2 on IX+ <i>I</i>	—	—	57+4	4	2	17.29.31	18.43	69
—	1 from IX	9 on IX	6	—	<i>I</i>	17.01.08	18.32	63
2 on X+ <i>I</i>	—	—	53+ <i>I</i>	13	—	15.46.32	18.30	73
—	(+1)+1 from X	—	—	—	—	11.39.31	18.34	3(+1)
9	3.4	(+1)+ x	71(+1) 5(+ <i>I</i>)	276(+1) 8	69	5	—	—
								90(+ <i>I</i>)

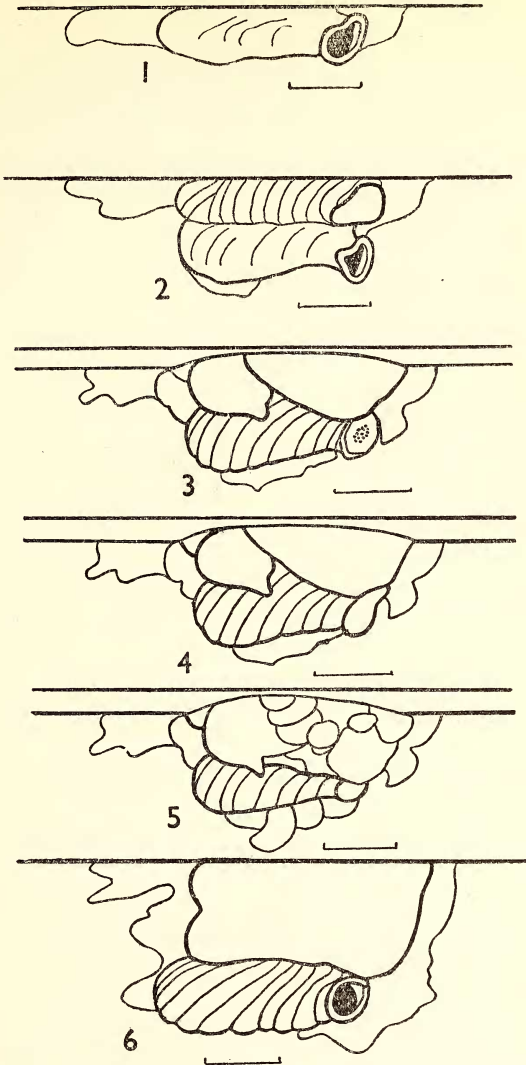
immediately before and during relevant activity, except for first and last inspections of day which

the cell with most of her body inserted. She left at 09.24.39. This long period on the nest, involving both intensive inspection and pauses, is characteristic of those visits which involve the removal of a concave lid. On only one occasion (26/7) were they not the first of the day. During the next 5 hours the wasp made 9 visits, on 3 of which she brought a spider, on 5 of which she brought nothing, but inspected both the inside and the outside of the cell, and on 1 of which it is uncertain if she brought anything (Table I).

The visits on which prey was brought to the cell were interspersed with inspection visits, and both kinds of visits were preceded by absences of irregular length sometimes of more than an hour. On 9 occasions during the 14 days of observation the wasp had inserted her head into the cell before the observer could be sure whether she was, or was not, carrying an animal. After our experiences on the first two days we are sure that loads must sometimes have been missed. We did not notice a stereotyped landing pattern, as Shafer (1949) did in specimens of *S. caementarium*; our wasp landed either on the table, or on any part of the construct. However she did have a stereotyped departure, always running to approximately the same place on the wood before taking off. At 14.23 she closed the cell with another concave lid. Rain did not start until 16.12, and was intermittent.

18/7. The second concave lid of cell II was again removed at the first visit. During the next 5 hours she made 1 inspection, brought 1 spider, made 7 inspections, brought 2 spiders, and with 3 loads of mud made the knob or convex lid shown in Fig. 4. After 2 more inspections she *daubed* the lid. She then put a similar daub elsewhere and one more on the lid. She then entered a period of *daubing*. This activity was more rapid than wall building. The ball of mud was put with some violence ('slapped down'), at first on the cells, and later on the previously deposited roughcast. She sometimes carried her ball for some seconds, sweeping actively over a large area before depositing it. She sometimes swept after deposition; but among daubing visits alone were a few where no sweeping *at all* was performed. She worked fairly systematically from above downwards, covering the structure built on the 16th. Once she left this structure and re-daubed lid II. The roughcast completely covered the cells, hiding their individuality and uniting them into a single block. The wasp's mechanics were sympathetic, in the sense that the observer could usually appreciate a reason for a daub being put where it was; the observer had been able to see an irregularity of edge or of surface which the daub obliterated.

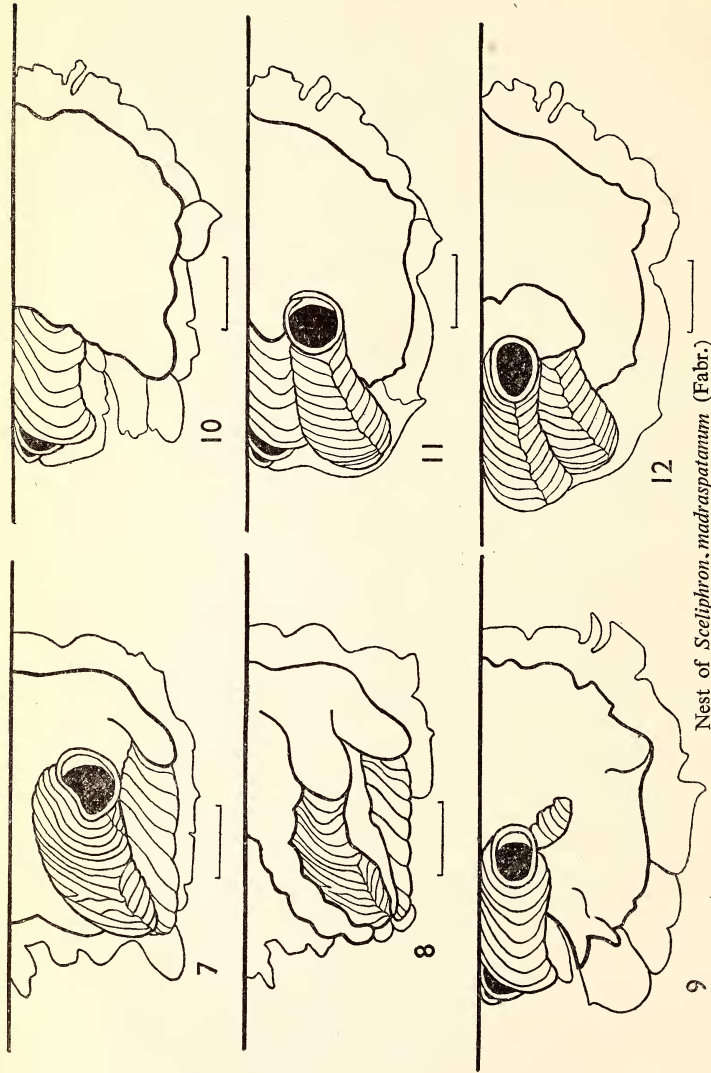
During such a daubing period some balls of mud were spread as a thin film on the table. During the period discussed on 18/7 all but



Nest of *Sceliphron madraspatanum* (Fabr.)

1. 15-7-60, 10.06.59. Cell I newly built and open. 2. 16-7-60, 10.57.46. Cell I sealed by permanent convex lid. Cell II newly built and open. 3. 16-7-60, 14.00. *seen from below*. Cell II sealed by 1st temporary concave lid. Cell I daubed with roughcast. 4. 18-7-60, 13.58.35. *seen from below*. Cell II sealed by permanent convex lid. 5. 18-7-60, 14.48.51. *seen from below*. Roughcast extended to partly cover cell II and convex lid. 6. 18-7-60, 16.51.38. Cells I and II completely covered by roughcast. Area of smeared mud extended. Cell III newly built and open.

(The small horizontal line below each figure represents 1 cm.)



Nest of *Sceliphron madraspatanum* (Fabr.)

7. 19-7-60. 16.03.38. Cell III closed by permanent convex lid. Cell IV newly built and open. 8. 20-7-60. 14.47.11. Cell IV sealed by permanent convex lid. Two new longitudinal bands of roughcast. 9. 21-7-60. 10.07.23. Cell IV almost completely covered by roughcast. Area of smeared mud extended. Cell V newly built and open. Note false starts of cell V which is insufficiently fore-shortened. 10. 21-7-60. 16.23.45. Cell V permanently sealed and area of roughcast extended over convex lid. 11. 22-7-60. 8.11.47. Cell VI newly built and open, and again insufficiently foreshortened. 12. 22-7-60. 12.59.47. Cell VI permanently sealed and convex lid daubed over. Cell VII newly built and open and again insufficiently foreshortened.

one were spread where the next cell, cell III, was immediately built upon them. They are therefore classified as *foundations*. One load however was placed elsewhere. Such an action is called a *smoothing*. A foundation and a smoothing are physically the same complex spreading movement, and were first distinguished by their final function in the nest. The distinction was confirmed by two observations; firstly the duration of a period of foundation building was about a quarter as long again as a period of smoothing though both periods showed a very similar amount of variation (Table IV). Secondly, the wasp was away significantly longer when fetching mud for a foundation than for a smoothing (Table V). At the close of a period of daubing and smoothing activity the observer could usually recognise where the next cell would be constructed by a concentration of spreading movements in one region. Usually after an absence (on 18/7 it was of 1863 seconds) the foundation loads became predominating and the walls were begun. The wasp completed cell III without pause and left for the night (Fig. 6). Our wasp therefore did not behave like those described by Fabre (1924) and Dutt (1913). The latter state, that all *Sceliphron* species including *madraspatanum* complete all the cells in a nest, then roughcast them all together, and desert the construct immediately¹. Our wasp, all told, had 7 periods of intensive daubing, and a few occasional loads were daubed on between these.

Dutt (1913) also considers that the smeared mud surrounding the block is the result of the wasp dragging her mud balls over the surface. We agree with Horne (1872) that these smears are deliberately made. The smoothing-foundation activity was very characteristic, and took more time than daubing (Table IV). We are sceptical of Horne's

¹In 1961 another nest was found in the same room. Unfortunately this was found after emergence of the imagines, so that we cannot be dogmatic that it belonged to *S. madraspatanum*. However in cell structure it resembled the nest that we have described, but unlike ours it confirmed Dutt's statement about the timing of what we call block daubing. This nest contained 21 cells, one vertical row of 8 being laid flat on the wood and two others of 7 and 6 respectively being built on top of them, so that the long axes of all cells were parallel. The cell which must have been the last built, whatever the hypothesis of the order of construction, was completely empty, and had never received a permanent lid. As it thus resembled our cell X (p. 13) this nest also seems to have been deserted unfinished. All the other cells had been permanently sealed, and the lid daubing was conspicuous covering the rims of the ridged cell walls for, as Dutt would have expected, no other part of the construct had been covered or embedded. This nest therefore also confirmed our association of the lid daubing with cell construction (p. 23) not with the block daubing which in our nest often followed it immediately. Dissection of the nest confirmed that the cells had been built directly on each other, the outer wall of one forming the floor of those above it, without, as in our nest, any daubing between. Fifteen cells had emergence holes in their lids and contained broken cocoons and two kinds of faeces exactly like those described on (p. 16). The remainder whose permanent lids were unperforated were filled with dried spiders and strongly suggested that no egg had been hatched, or perhaps laid, in them.

suggestion that the smeared mud has a cryptic function by resembling splash, and our animal, unlike his, made no isolated 'drop' marks. The mud was carried daintily in the mandibles high above the surface of the substrate, and the wasp often swept for some time before she deposited it. Indeed the mud was of such a consistency that most of any load would stick where it first touched.

19/7. The wasp first made 2 inspections separated by 7018 seconds, departed for 4450 seconds, returned with a spider, made a single ovipositional entrance, then made an imperfectly seen visit, and 2 inspections. She then brought a *fly* of a small grey waxy sarcophagine-like species. The fly was carried parallel to the wasp's long axis under her body. Its russet eyes were visible under her head, and so were the segmented abdomen and the wings crushed together under the much more slender abdomen of the wasp. That flies are prey for members of this genus confirms the observation of Rukov which Kohl (1918) quotes with derision. She then brought 3 undoubted spiders and immediately sealed the nest with a convex lid built of 4 loads of mud, and obliterated it with 2 daubs. After 1 load smoothed on the wood, she spread 4 loads consecutively: these proved to be foundation of cell IV, or more correctly the foundation of the *end* of cell IV, because cell IV was the first to be built mainly overlapping the previous construct. She made 4 visits building the walls of cell IV, but on her next visit she pushed her load of mud behind outside the upper rim. She finished the cell with 23 more loads, left for 4627 seconds, made a short inspection (14 seconds) and left for the night (Fig. 7).

20/7. She began the day with 2 inspections separated by 6247 seconds. She then brought one load of mud and added it to the upper wall of cell IV. After 2848 seconds she brought a spider, oviposited, and then spent 10 minutes inspecting the outside. She then made a visit in which the load was uncertain, then 2 inspections, and then 2 more visits on which she again brought *flies*. Then, after a doubtful visit, she made 3 inspections and closed the nest with 3 loads of mud, making a convex lid. She then joined this lid to the block, partly obliterated it with 3 more loads, and began roughcasting in two bands, one above and one below the newly sealed cell IV. While doing this, she added 3 daubs specifically to the convex lid of IV, and smeared 3 loads on the table, one of which became part of the foundation of cell V. Her last departure was after the light had begun to fail and heavy rain was, correctly, anticipated (Fig. 8).

21/7. She opened the day with one inspection, put a load of mud on lid IV, and then made 31 visits daubing mud, covering cell III completely, and almost covering cell IV. Among these she made 5 visits spreading mud on what proved to be the foundation of cell V, and 11

smoothing mud elsewhere on wood, including that to the north or window side of the construct in front of the sealed mouths of II and III. After being absent for 1566 seconds she inspected and then made 14 foundation building visits among which were 2 daubing and 2 smoothing visits. She then constructed the walls of cell V, between cell IV and the table top. For details here, and in the rest of the description of construction, see Table I. The first few arches of the upper wall remained outside the final cell (Fig. 9). She oviposited, provisioned with spiders, and sealed with a convex lid which was immediately joined by daubing to the part of the block already constructed (Fig. 10).

22/7. This day was the peak of her productivity. She made 214 visits and worked for 10 hours 10 minutes. She began with an inspection, and built cell VI immediately (Fig. 11). During this she made two daubs, probably necessary architecturally for the cell construction. At the beginning of this building we moved the left, or south, corner of the table away from the wall so that the wall and the back edge of the table made an angle of about 14° , i.e. the nest had been turned slightly towards the window. This removed the south side of the nest, where building was being done, from the shadow cast by the completed part. On the next visit, the wasp approached about 10-12 cm. to the left of the nest, but immediately doubled back to land on it. The wasp oviposited in cell VI only just over an hour after her first arrival in the morning, put in 5 spiders, sealed it permanently with a convex lid made from 4 loads, and began the foundations of cell VII before she finished daubing the lid. She built cell VII, again including a few daubs on the block (Fig. 12), left for almost an hour, and brought a spider. She made an ovipositional entry, then removed the spider and tried again. She then threw the spider out, swept, and left to return with another after 1065 seconds, and repeat the complete entry abdomen first. She added one more spider and sealed the cell with a concave lid made from a single load. It was then 14.45. She then brought 114 loads of mud, 80 of which she daubed, and 34 of which she smoothed, some of them on the vertical edge of the table top itself. The appearance of the block and the area of smoothed mud surrounding it was entirely altered (Fig. 13). On this occasion alone she roughcasted a cell which was incompletely provisioned. She left a distinct groove from the edge of the table top to the rim of lid VII which she used next morning to insert her mouth-parts to bite the lid off. During this period of intense construction she made three visits purely to inspect.

23/7. The day started with heavy rain. The animal arrived 5 minutes after sunshine was first noted, and after sweeping, removed the concave lid of cell VII. The cell was provisioned. The abdomen of

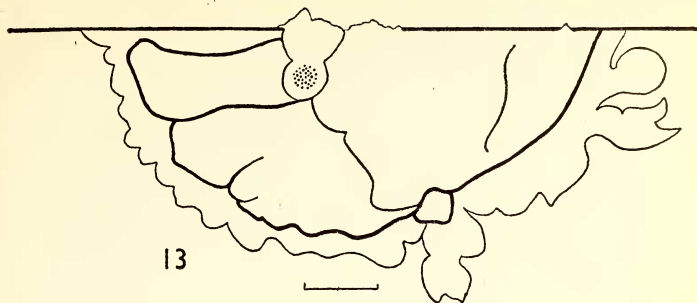
the last spider brought was too large to enter the hole and a 2-minute long struggle was seen. First the spider was pushed in head first as usual. Then it was deliberately turned round and an attempt made to push in the abdomen. The spider dodged the hole actively, and walked away carrying the clinging wasp. The wasp finally dropped the spider and spent nearly 3 minutes wiping her body and sweeping the block. The spider was motionless when retrieved from the floor by the observer. One inspection visit was then made, and then surprisingly, the cell was sealed permanently. This convex lid was left undaubed, probably because it rained for the rest of the day.

24/7. After the usual initial inspection visit, the animal brought mud and completed the lid on VII by daubing on it. After one more daub on VII the wasp built cell VIII (Fig. 14), oviposited, provisioned, permanently sealed it; and promptly built cell IX leaving it empty and open for the evening (Fig. 15). Only 1 load was spread on wood as a foundation for VIII and only 2 for IX. These two cells were built almost entirely over the previous ones. Cell VIII also showed some imperfections in its walls.

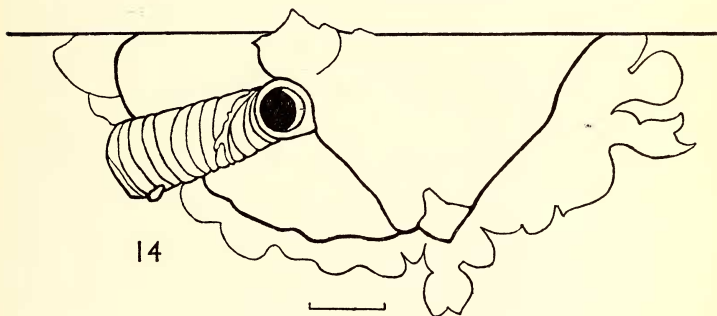
25/7. After the first inspection, she laid in cell IX and another spider was introduced. There were many inspections. The cell was then sealed temporarily with a concave lid. Within 2 minutes of completing this, heavy rain and thunder began. The wasp returned over an hour later, within 10 minutes of the rain ceasing, and daubed mud covering cell VIII and part of cell IX (Fig. 16). After more rain, she made her last visit, a curious inspection lasting 917 seconds. It contained two pauses during which she was motionless for 3 minutes. She repeatedly returned and swept the lid of cell IX, as though she had a guilty conscience about leaving it.

26/7. Today the wasp did not remove the concave lid at her first visit but at her second, which was 1766 seconds later and involved much inspection. After gnawing round the lid she seemed to kick it off because it did not fall vertically. Cell IX was further provisioned, and sealed permanently with a convex lid, roughcasted over as usual. Foundations of cell X were begun, alternating with this lid daubing, but 6 generalised daubs were also made before the cell walls were begun. These could not be interpreted as preparing the block surface for cell X. Cell X was built immediately (Fig. 17). The day ended with an inspection, 2 hours and 40 minutes after the last load of mud had been brought. The weather was sunny during this intervening period.

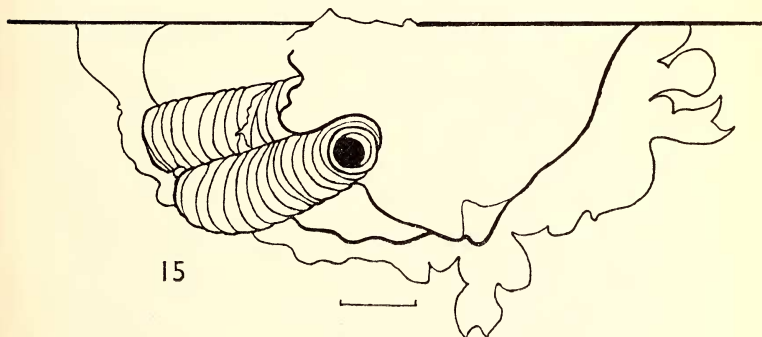
27/7. After the morning inspection visit, oviposition took place in cell X. She then re-entered the cell head first, then again abdomen first carrying a small flake of mud with her. Four more spiders were



13



14

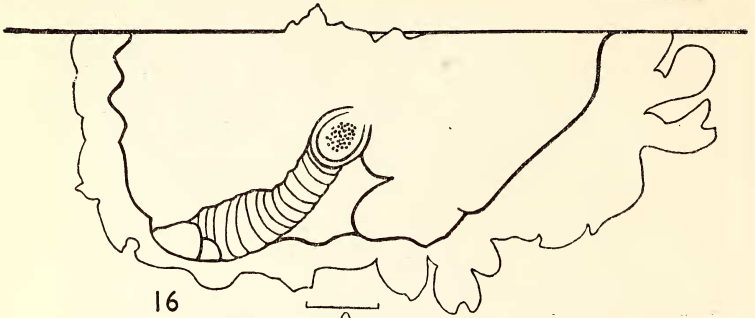


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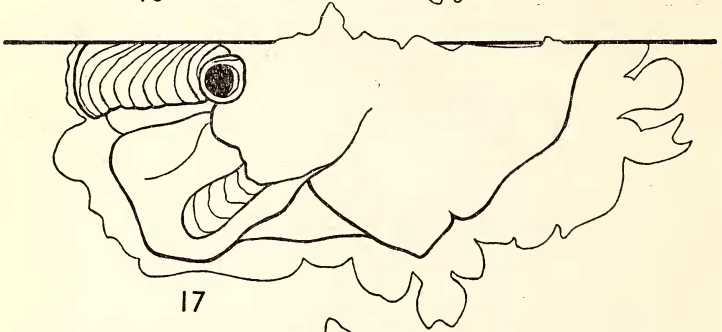
Nest of *Sceliphron madraspatanum* (Fabr.)

13. 22-7-60. 17.13.32. Cell VII sealed by temporary concave lid to which ridge runs through roughcast to facilitate it being bitten out next morning. Cells VI and VII covered by roughcast and smeared area much enlarged especially to observer's right. 14. 24-7-60. 9.15.10. Cell VII sealed by permanent convex lid which has been daubed over with roughcast. Cell VIII newly built, open, insufficiently foreshortened. Note imperfection of walls. 15. 24-7-60. 15.53.28. Cell VIII sealed by permanent convex lid which has been daubed with roughcast. Cell IX newly built and open.

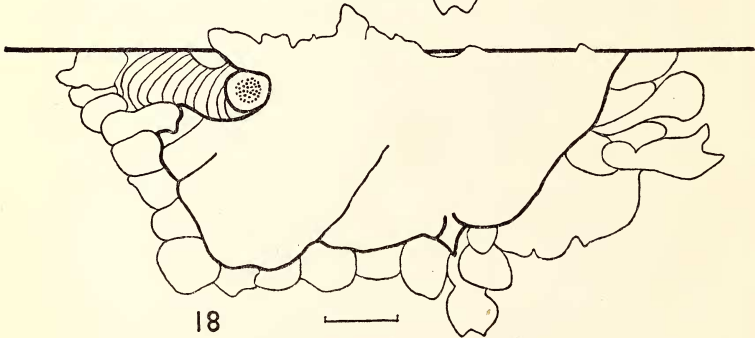
(The small horizontal line below each figure represents 1 cm.)



16



17



18

Nest of *Sceliphron madraspatanum* (Fabr.)

16. 25-7-60. 17.29.21. Cell IX sealed by temporary concave lid. Cell VIII completely covered by roughcast. 17. 26-7-60. 15.18.47. Cell IX partly covered by roughcast. Cell X newly built and open. 18. 27-7-60. 15.46.32. Cell X sealed by temporary concave lid. Cell IX completely covered by roughcast.

(The small horizontal line below each figure represents 1 cm.)

introduced, the cell was closed by a temporary concave lid and the wasp immediately daubed cell IX completely, interspersed with the smoothing of mud to the south of the block.

28/7. At 06.39 the observer found the wasp already on the construct. This morning she spent most of the time waving her antennae in the air rather than sweeping. She spent several isolated periods absolutely still, one of about 5 minutes. After being watched for 10 minutes she bit the lid. She was then deliberately disturbed by being blown upon, and, after hovering over the construct, left. She had thus been on the construct over 625 seconds before beginning lid removal, most of which time she was motionless. On the 4 previous occasions on which lid removal was seen, she had not only been extremely active but on 2 had begun biting in under 1 minute from arrival, in 1 in under 2, and in the fourth, from cell VII, had begun biting in about 4 minutes. Therefore, before she was disturbed she was behaving abnormally, by being lethargic. This doubly incompletely recorded visit is not considered in Table IV.

She returned after 2399 seconds, examined the cell for 916 seconds during which she was again motionless for periods of 2, 6, and 2 minutes. She took just under 290 seconds to remove the lid, during which time she walked away from it once and left after 50 seconds of inspection. This complete visit, which almost certainly would not have occurred if the animal had not been disturbed on her previous visit, is considered in Table IV.

After 1 inspection she brought a spider, and was then interrupted by rain, followed by 1 inspection and 1 spider after more rain. She made 3 more inspections, the last after an interval of 4300 seconds during which there was no rain. Rain was recorded during the afternoon, but there were also long sunny periods. Watching was discontinued at 18.35.

29/7. The nest was watched from 06.13 to 13.38. There was again rain, but neither in duration nor in intensity sufficient to stop her, judged by previous days. No further addition was seen to the construct.

There are two interpretations. Either the wasp deserted the nest, perhaps because the gust of air produced by a human blowing gently had an unexpectedly great valence for her, and a valence quite different from that of the occasional unintended disturbances caused by sudden movements of the observers. If this is so, two aspects of her behaviour are unexpected; she neither deserted immediately, nor, alternatively, brought the provisioning for her last offspring to a satisfactory conclusion. Alternatively, we may interpret her languor, seen before the disturbance, as a sign of senility, or malaise, so that she did not desert, but died, perhaps being too slow to escape a predator. If

she was becoming senile, it is curious that she arrived at least 30 minutes earlier than on any previous day. Perhaps we have missed visits in the early mornings, even after 16/7, but these could only have been visits of inspection.

The data collected on the 14 days are summarised in Table I. The building activities are set out in the functional order of the building, provisioning, and sealing a cell, though only on 15/7, when it was not observed, and on 22/7, was the first activity foundation building. Inspection visits except for the first and last of the day have been associated with the chore which they *preceded*.

Most activities are performed in bursts, and the order of these bursts is shown in Table I. However, the irregular alternation of 'certain' prey and 'doubtful' prey has not been shown, nor the irregularity of lid daubing, block daubing, smoothing, and foundation spreading. This can be generalised by saying that the wasp gradually transfers her attention from the lid she has just sealed to the construct as a whole, and then her attention gradually narrows to the place where her next cell will be built. Dutt (1913) records that he scraped off the two cells which he found in a particular nest. As the wasp daubed over the surface he had broken and, as Dutt considered that daubing is only done before the nest is finally left, he suspected that the daubing follows 'a set routine'. We disagree; and once a cell is sealed we consider that the consummatory stimuli (as the ethological school following Sherrington would call them) sought during daubing are provided by the suitability of the construct as a whole to receive another cell, *not* by the disappearance of the cell being covered.

31/7. 19.00 approximately. The contents of cell X were noticed very near the cell mouth, and at about 20.00 the larva of X was found on the floor. It was quite motionless, and it was preserved.

1/8. 10.30. The entire table was removed to an insect cage out of doors which was covered by a tarpaulin. At 14.15 the temperature under the tarpaulin was 47°C. Therefore the table was sawn up and the nest, still attached to the wood, was stored resting on blotting paper, in a large glass jar covered with muslin.

Seven wasps emerged, all perfect. They were killed a few hours after emergence. Details are given in Table II. The diameter of the emergence holes was about 4 mm., i.e. much less than the diameter of a newly finished cell mouth. The lids removed were in the same place as the lids constructed by the mother, and were surprisingly thin flakes, considering the thickness of the mud layer with which the cells had been sealed and individually roughcasted. The lids were cut almost, but not quite, all round their circumferences and were left on cells VII, VIII, and IX, those from VII and IX being left parallel to the

surface of the block and in a position that still partially closed the exit to the cell. When the nest was dissected on 3/5/61 it was discovered

TABLE II

PARTICULARS OF EGG-LAYING AND EMERGENCE

Cell	Laid	Emerged	Length of pre-imaginal life in days	Sex	
I	15-7, a.m.			♂	see text
II	16-7, ,,	5-8, a.m.	20	♂	
III	19-7, ,,	8-8, ,,	20	♂	
IV	20-7, ,,	9-8, ,,	20	♂	
V	21-7, ,,			♀	see text
VI	22-7, ,,	12-8, ,,	21	♀	
VII	22-7, p.m.	11-8, ,,	19.75	♀	
VIII	24-7, a.m.	13-8, noon	20	♀	
IX	25-7, ,,	14-8, p.m.	20.25	♀	
X	27-7, ,,			?	see text

that the cocoon in cell I was in a reversed position, the faecal cup being proximal to the lid; that a tunnel 4.5 mm. long had been bored from distal end of cell I, into the wall of cell V which contained a crushed female pupa, presumably V, facing its component lid, and a male wasp, with expanded wings, presumably I, facing away from lid V. Both were dead.

The length of pre-imaginal life was remarkably constant and the same for both sexes though perhaps more variable in females. It was about 3 days less than the minimum Dutt (1913) observed in specimens of this species at Pusa in Bihar. That all the males emerged before all the females is an example of the proterandry that Kohl (1918) expected would be found among *Sceliphron* species. However, at least for this sibship, the explanation is *not* that the males develop more rapidly than the females but that *all* the male eggs (4) were laid before all the female eggs (5) (*protarrhenotoky*, Jayakar 1963) an observation expected to be made by chance once in 126 times. If males are haploid, as they are in all Hymenoptera studied (White 1954 p. 326), the fertilization of the wasp observed *may* have occurred after the

construct was half built, and this fertilization may have stimulated the great burst of activity on the 21/7 and 22/7. Alternatively some maturation of the female's spermatheca, or of the sperm within it, may be necessary in this species before fertilization can take place. There are other possible explanations. The dissection of the nest revealed the cocoons. In this species, these resemble those described by Fabre (1924), being of a thin russet lac-like substance suspended by white silk threads from the mud wall, which was itself thinly lined with silk. We disagree with Dutt (1913) that the cocoon is spun. Spun threads were rare in samples we have examined. The cocoons were rounded and broader at the end which covered the head and thorax of the pupae, and which except in cell I lay proximal to the lid. At the distal end the cocoon narrowed to a hard black cylindrically walled cup about 2 mm. in diameter, and about 3 mm. deep. These cups contained an earthy substance which was debris of arthropod cuticles. This confirms Dutt (1913) who claimed it to be larval faeces. However, among this debris in the two cups examined, a small fibrous moulded lump was found of a different shape in each case. This seems to be the unused lac which Morley (quoted by Kohl 1918) states is excreted into these cups. On the surface of this debris we always found a larval moult. Only in one cell did we find any structure which might have been a pupal moult. This, therefore, seems usually to be eaten, or must be very inconspicuous. Finally, in all cells but I, II, and V, we found a layer of fusiform white pellets. Further pellets were found loose in the cell, and they were also found on the floor of the glass jar. Shafer (1949) observed that in *S. caementarium* such pellets were present in the larval tissues, gradually increasing in number during development, so they can only in part be a meconium due to the metabolism of metamorphosis, though they are not passed until after the emergence of the imagines. The cocoon was messily broken, and sometimes in fragments at the head end. In cell V the head end was complete, and the rupture was distal and seemed not to have been made by the occupant, but by wasp I who was an intruder in cell V.

III. ANALYSIS

Table III presents a summary of those loads assumed useful to the developing larvae; i.e. inspections, removals, and unsuccessful introductions of prey have been omitted.

The separation of *foundation* from *smoothing* first made on function is justified by the observation that the animal spends more time on the former (Table IV). That the two means have very similar variances suggests that they have been accurately separated during recording.

TABLE III
LOADS ACTUALLY USED ON THE NEST

2	Larva	Foundation	Walls	Spiders and flies inserted, incl. oviposition	Doubtful prey	Sum of possible prey	Concave lid	Convex lid	Daubs on convex lid	Daubs	Smooths	Sum of daubs and smooths (2 odd loads omitted)
	I	x	25+?	2	8	10	2	3	2	x	x	..
	II	9	22	6+?	1	7	x
	III	13	24	5	1	6	2	3	4	29	1	30
	IV	5	28	3	2	5	..	4	2	..	1	..
	V	20	29	9	2	11	..	3	7	45	15	60
	VI	5	25	6	..	6	..	5	7
	VII	11	26	4	3	7	..	4	6	85	35	120
	VIII	1	31	12	1	13	1	4	3	1
	IX	2	24	9	1	10	..	3	3	58	4	62
	X	14	29	7	0	7	2	3	6	59	13	72
	Mean	8.9	26.3	6.3	..	8.2	68.8
	σ^2	33.9	8.0	9.3	..	6.8	..	0.5	4.25	1065.2
	C. O. V. %	65	11	49	..	32	..	19.6	47	47

Identifying and classifying journeys associated with walls, oviposition and prey, and the two lids presents no difficulty. Daubing is a characteristic activity, but it is not associated with one cell at a time. A few daubs seem to have been put on separately to improve the surface for a cell under construction, or at least, in contemplation. In Table III daubing and smoothing visits are classified with the cell which had last been *permanently* sealed with a convex lid. On 4 occasions the next cell (II, VII, IX, X) also had been temporarily sealed after partial provisioning. Only cell VII on 22/7 was covered with daubs to any great extent before being permanently sealed. Some figures in Table III are as might have been expected from the function of the chore to which they refer. It seems reasonable that the number of loads used to construct a foundation should be variable while those used to construct the cell walls should be constant, because the function of a foundation is to respond to exigencies, whereas the function of a cell is the *raison d'être* of the whole structure, and this does not differ from cell to cell. Similar considerations would lead us to expect the observed standardisation of the number of loads used to make the two kinds of lid, and the variability of the number used in both lid and cell daubing and smoothing.

Fabre (1924) counted 15-20 ridges on the cells of the European species diagnosed now as *spirifex*. He considered that each ridge represented one load. In *madraspatanum* at least, a ridge represents two loads. If this is so also for *spirifex* the cells of the two species require a similar amount of work to build, though those of *spirifex* are about 0.5 cm. longer. The numbers of prey are smaller than those given by previous authors, 11-24 by Shafer (1949) for *S. caementarium*, and 'about 18' by Dutt (1913) for the present species. What is surprising is the great variation in the numbers introduced. Table III shows that this variation can be very little an artifact of our doubts as to how many there actually were. This variation surprised us while observing; we were never able to predict when the wasp would be satisfied and seal the cell. Many species of spiders are used, and one large must be equivalent to many small, but this was not obvious during watching, and cannot always be appreciated by the wasp. For example the spider that escaped from cell VII on 23/7 was the last brought and, after one inspection, the cell was sealed. There was no compensation for this, the largest spider seen, which she had at one time intended to introduce.

The duration of the periods spent on the cell is an indication of the difficulty of, or care taken with, the work. These periods consist of two components, not consistently separated in the record. Firstly the time taken 'handling' material, and secondly the time taken deciding where to put the load, and/or examining it in position. This

TABLE IV
DURATION OF TIME IN SECONDS ON CELL

Operation	Visits seen	Visits timed	Smallest	Largest	Mean	IQR Median %	c.o.v. %	Median	s.e. of Median Estimate	
									1	2
Daubing block	277	276	9	129	27.18 ± 0.90	47	55.1	23.70	0.46	0.66
Daubing lid	40	40	9	125	33.73 ± 4.34	85	81.3	23.50	1.84	2.95
Smoothing	69	69	12	91	35.55 ± 1.66	52	38.8	33.25	1.56	1.93
Walls	265	263	20	246	44.56 ± 1.13	34	41.0	41.60	1.01	0.85
Foundation	80	80	18	98	46.76 ± 1.94	49	37.2	45.17	3.72	2.30
Convex lid	32	31	26	169	53.94 ± 6.65	92	68.7	38	6.65	4.73
Concave lid	9	9	46	244	126.56 ± 24.08	104	57.0	126	24.08	40.26
Lids combined	41	40	26	244	70.23 ± 8.76	137	78.8	45.375	3.16	9.24
Doubtful prey	19	19	10	82	35.05 ± 4.38	74	57.9	31.0	—	—
Certain prey	55	55	11	315	55.25 ± 7.74	64	104.4	40.25	—	—
Oviposition	12	12	47	720	172.50 ± 52.0	53	104.5	106.5	—	—
Inspection	91	90	8	917	87.13 ± 14.00	156	152.6	42	—	—
Lid removal	6	5	335	1307	695.60 ± 163.59	—	52.6	625	—	—

examination often seems to include deciding where to place the next load. The latter component seems more variable than the former, and the extremely long visits that sometimes make the median a more useful statistic than the mean, owe their length almost entirely to the sensory or inspecting component. The times spent *away* from the cell before a given activity can be similarly analysed. If the activity on the cell involved bringing a load, some of the time away must have involved finding it and, when an animal had been only 8 seconds away when she returned with a ball of mud, we may assume that she spent most of the time collecting the mud. However, the existence of extremely long absences suggests that the wasp sometimes performed other activities besides collecting while she was away.

Our wasp's quantitative behaviour while on the nest was probably typical of the species in this climate, as we assume her qualitative behaviour to have been, but the times during which she was away must have been very closely determined by the nearness of suitable mud, and perhaps, but less certainly, the ecology of the local spiders, i.e. these periods will differ from locality to locality, and season to season, and must not be assumed to be characteristic of the species.

Tables IV and V summarise the data on periods, on and away from the cell respectively. In Table IV the mud carrying activities have been ranked in order of mean length of durations, beginning with the shortest, i.e. *block daubing*. The order judged by the median is similar, and for the *lid building*, where there were a few extremely long visits, more informative. For the other visits, *bringing prey*, and *inspecting*, the mean and median are surprisingly near together considering the small totals, and the variation.

The durations of absences were so skew that the mean is meaningless. Therefore ranking in Table V has been performed on the medians.

Considering the work with mud, these rankings suggest generalizations. However, comparisons require some measure of the reliability of the statistics. There is no satisfactory formula to estimate the standard error of a median, and the differences between the values obtained by the use of various *ad hoc* formulae reveal that the assumptions on which they are based are not true of the populations concerned.

Estimate (1) was calculated from the formula $\frac{1}{2\sqrt{n}} \cdot \frac{1}{f_c}$, where f_c is the median ordinate and is estimated from the central 5 or 6 values in the sample, depending on whether n the total sample size was odd or even. We are thus assuming regularity of the sample just around the median. The abnormally high standard error of *foundation making* is due to an irregularity in this region, which, knowing our